

NEW MATERIAL OF AN EARLY CRETACEOUS TITANOSAURID SAUROPOD DINOSAUR FROM MALAWI

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ABSTRACT. Compared to their Late Jurassic record, sauropod dinosaurs are poorly known in the Cretaceous Period between 144 Ma and the terminal Cretaceous extinction event at 66 Ma. The Titanosauridae are the most widespread and common of Cretaceous sauropods. The titanosaurid species from the Dinosaur Beds of Malawi, Africa, here referred to *Malawisaurus dixeyi* comb. nov., has procoelous anterior caudal vertebrae, a characteristic of the family, but middle and distal caudals with gently biconcave ends. Caudal neural spines are low, a feature that is shared with South American *Saltasaurus* and North American *Alamosaurus*. A premaxilla of *Malawisaurus*, the first known for the family, is primitive in having the external nares placed far anterior, demonstrating that this titanosaurid has a blunter snout than other sauropods. Flattened teeth in *Malawisaurus* suggest that pencil-shaped teeth may have evolved more than once within the Sauropoda. Titanosaurids probably originated at a time when other sauropod families were differentiating in the Late Jurassic. The Titanosauridae is the longest lived group of sauropods.

IN a comprehensive review of sauropod dinosaurs, McIntosh (1990a) recognized six families. Among these are the Diplodocidae, containing the familiar genera *Diplodocus*, *Apatosaurus* and some others, the Brachiosauridae, or giraffe-necked sauropods, including the gigantic *Brachiosaurus*, the Camarasauridae, the two primitive families Vulcanodontidae and Cetiosauridae, and the Titanosauridae. All of the sauropod families were in existence by the Late Jurassic, but their origins and interrelationships are poorly understood. Among the most enigmatic and least understood of these groups is the latest surviving Titanosauridae (McIntosh 1990b), which is the most widely distributed, and last surviving of Cretaceous sauropods. It is unique among sauropod families in that its members possess dermal ossifications or scutes.

Titanosaurids were first recognized from the Late Cretaceous of India, and the oldest known generally accepted titanosaurid record is from the Late Jurassic of Africa. They are known from Madagascar and Europe, and titanosaurid remains are numerous in the Late Cretaceous of South America. The family includes the last recorded sauropod in North America, *Alamosaurus*, from Texas, New Mexico, Utah, and Wyoming.

Titanosaurid dinosaurs from Malawi (previously Nyasaland), Africa, were first described by Houghton (1928), who named *Gigantosaurus dixeyi*. No significant new collections were made in Malawi until the initiation of a joint Southern Methodist University (SMU) and Malawi Department of Antiquities programme in 1984 (Clark *et al.* 1989; Jacobs 1990; Jacobs *et al.* 1990, 1992). Since the inception of this project, approximately 150 dinosaur specimens, including both isolated bones and articulated sets, many of which pertain to sauropods, have been removed from nine localities in the Early Cretaceous Dinosaur Beds (Lupata Group) of the Sitwe Valley, near Mwakasyunguti, northern Malawi (Colin and Jacobs 1990; Jacobs *et al.* 1990). The purpose of this paper is to evaluate *Gigantosaurus dixeyi* using previously unknown skeletal elements, the premaxilla, dentary, ischium, middle and distal caudal vertebrae, and cervical vertebrae.

All the material described here is from one quarry (designated CD-9) and occurred within 30 square metres. Some of the bones, notably sternal plates, middle and distal caudal vertebrae, and some cervical vertebrae were found articulated, but other bones were scattered and isolated to some

degree. The quarries this project is working occur within the same rock units and in the same areas as the original collections made by Dixey (1928) and Migeod (1931*a*, 1931*b*), from matching Dixey's photograph (1926, unnumbered plate between pp. 120 and 121, labelled 'Looking across the Mwakasyunguti Valley from the southwest'). A faunal list from the Dinosaur Beds is given in Jacobs *et al.* (1990), but only titanosaurid material is discussed here. All the material represents a relatively small sauropod.

All specimens collected by our project remain the property of the government of Malawi; specimens with numbers preceded by MAL have been taken to Southern Methodist University, Dallas, Texas for study. Other designated specimens are housed in the Department of Antiquities in Malawi.

SYSTEMATIC PALAEOLOGY

Subclass ARCHOSAURIA Cope, 1869

Order SAURISCHIA Seeley, 1888

Suborder SAUROPODOMORPHA Huene, 1932

Infraorder SAUROPODA Marsh, 1878

Family TITANOSAURIDAE Lydekker, 1885

Emended diagnosis. The most diagnostic derived characters of the Titanosauridae include a transversely expanded ischium and strongly procoelous anterior caudal vertebrae. (Those vertebrae in the tail having caudal ribs or transverse processes are considered here to be anterior caudal vertebrae.) In more derived titanosaurids the middle and posterior caudals are also procoelous. Teeth are narrow, flattened in more primitive forms, but may be more pencil-like in derived forms. Sternal plates are robust. The neural spines of cervical vertebrae are undivided and the cervical ribs extend beyond the centrum to overlap the following vertebra, both of which are primitive characters. Teeth are not limited to the anterior portion of the jaw, at least primitively. External nares are far anterior.

Distribution. Late Jurassic of Africa; Early Cretaceous of Africa, Europe, and questionably South America; Late Cretaceous of Africa, Madagascar, South America, North America, Europe, and Asia.

Taxonomic note. All of the material described below pertains to the Titanosauridae, and there is no indication that more than one titanosaurid species is present in the Dinosaur Beds. The anterior caudals collected by this project appear to be specifically identical with that originally described and illustrated (Haughton 1928, pl. 3) as *Gigantosaurus dixeyi*. Haughton (1928) correctly considered the specimens he included in *G. dixeyi* to be most closely related to some of those called *Gigantosaurus robustus* from the Late Jurassic of Tendaguru, Tanzania.

Two species of *Gigantosaurus* had been named from Tendaguru, *G. africanus* and *G. robustus*, both by Fraas (1908). Unfortunately, the generic name was preoccupied so *Tornieria* was proposed to take its place (Sternfeld 1911); thus the species named from Tendaguru became *T. africana* and *T. robusta*. *G. dixeyi* from Malawi became known as *Tornieria dixeyi* without further justification. However, the species named *G. africanus* by Fraas (1908), the type species, was subsequently reassigned to *Barosaurus africanus* (Janensch 1922), leaving only *T. robusta* in the genus, which is nomenclaturally untenable. Therefore, the name *Tornieria* was changed to *Janenschia* by Wild (1991), so *T. robusta* is now *Janenschia robusta*. The taxon from Malawi is closely related to but distinct from the titanosaurid genus *Janenschia*. It is less closely related to *Barosaurus*, a diplodocid. For those reasons, a new genus is erected to accommodate the titanosaurid species from Malawi.

Genus MALAWISAURUS gen. nov.

Derivation of name. Named for the country of Malawi plus *-saurus*, Greek, for lizard.

Diagnosis. As for the only known species, *Malawisaurus dixeyi*.

Malawisaurus dixeyi (Houghton, 1928) comb. nov.

Text-figs 1–2

- v*1928 *Gigantosaurus dixeyi* sp. nov., Houghton, p. 70, pl. 2, figs 1–3, pl. 3, pl. 4 fig. 1.
 1932 *Tornieria* (*Gigantosaurus*) *dixeyi* Houghton; Stromer, p. 7.
 1954 *Tornieria dixei* (sic); Lavocat, p. 67.
 1987 '*Gigantosaurus*' (? = *Tornieria*) *dixeyi*; Raath and McIntosh, p. 117.
 1990a *Tornieria dixeyi*; McIntosh, pp. 352, 398.
 1990 '*Gigantosaurus*' *dixeyi*; Jacobs *et al.*, p. 200.

Holotype. The type is taken to be the anterior caudal vertebra illustrated by Houghton (1928) and catalogued as South African Museum no. 7405. The remainder of the material included by Houghton with the type (a right pubis, an incomplete scapula, and sternal plates) is considered topotypic.

Type horizon and locality. Upper member of the Early Cretaceous Dinosaur Beds (Lupata Group); Mwakasyunguti area, northern Malawi, Africa.

Additional material. Premaxilla, dentary, teeth, cervical, dorsal, and caudal vertebrae, sternal plates, ischium.

Diagnosis. A sauropod dinosaur having strongly procoelous anterior caudal vertebrae with short, vertical neural spines. Additional characters from topotypic specimens indicate middle and distal caudal vertebrae are not procoelous, the ischium is transversely expanded, cervical and dorsal vertebrae have undivided neural spines, haemal arches do not bifurcate, cervical ribs extend posteriorly beyond the centrum, the premaxilla is blunt with the external naris relatively anterior in position, teeth are not restricted to the anterior portion of the lower jaw, and there are at least 15 tooth positions in the dentary.

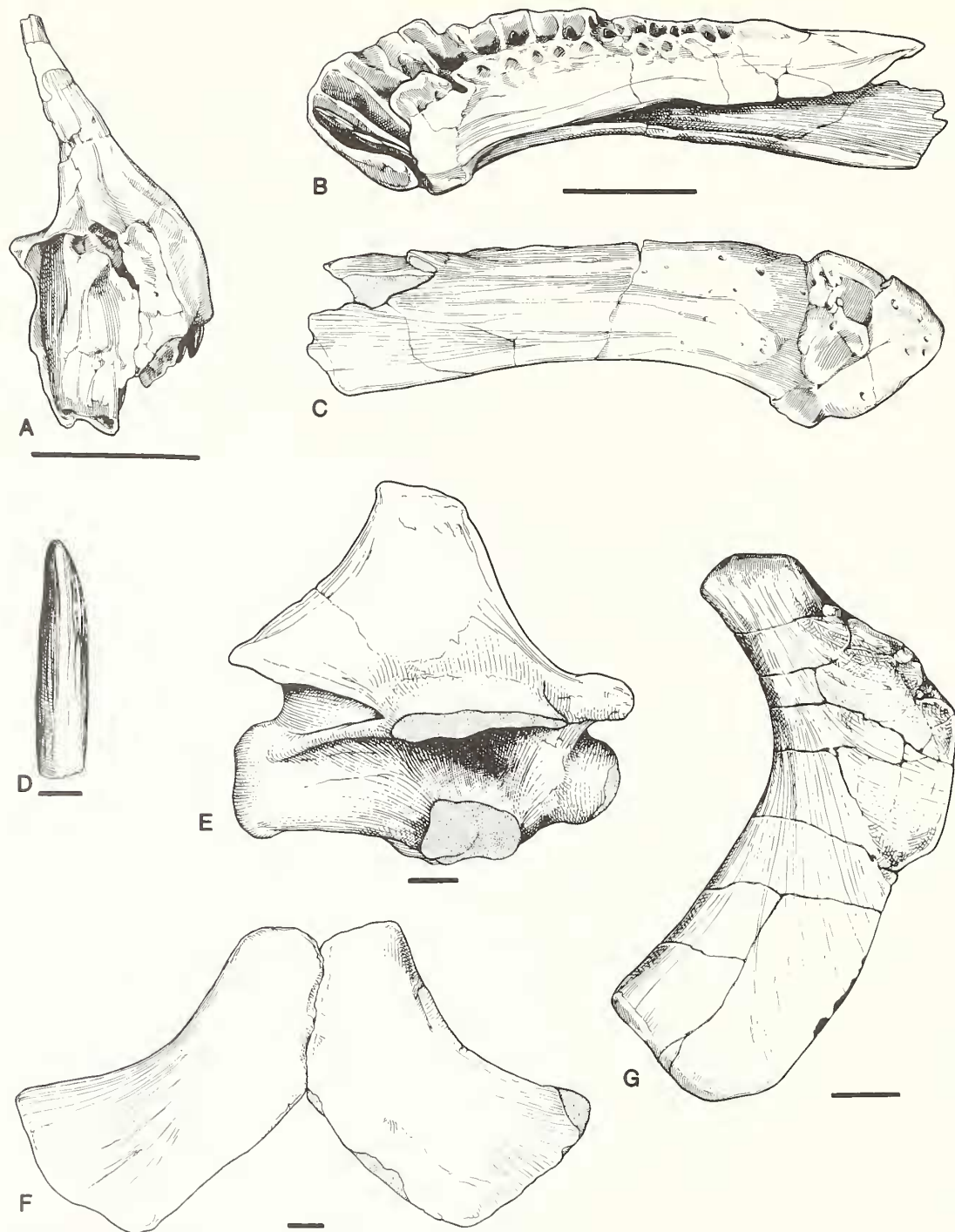
Description. An apparently nearly complete premaxilla (MAL-6; Text-fig. 1A) is robust. The alveolar margin of the premaxilla is slightly damaged, obscuring an accurate count of tooth positions. Three unerupted teeth are present. The premaxilla exhibits less anterior elongation than seen in *Camarasaurus* and much less than the projecting premaxilla of *Brachiosaurus*. The external naris is large and bordered anteriorly by a narrow, dorsally oriented ascending process. The maxillary suture is below the external naris, rather than extending anterior to it as in other sauropod taxa in which this feature is known. This premaxilla is therefore unique among sauropods, so far as can be determined. It demonstrates that the species it represents had a blunt snout and domed skull. The external nares were lateral on the skull, far forward, and less retracted than in *Camarasaurus*. The placement of the external nares was very different from the dorsal position of diplodocids and the dorsolateral condition of *Brachiosaurus*.

One dentary (MAL-174; Text-fig. 1B–C) has 15 tooth positions (minimum). Eight unerupted teeth can be seen (tooth row length = 175 mm; length from symphysis to surangular notch = 201 mm; height of dentary at mid length = 51 mm. The posterior tooth position is 23 mm anterior to the notch for the surangular. Anteriorly the dentary is gently curved towards the symphysis. The splenial groove on the medial surface is broadly open posteriorly, tapering forward to a level approximately below the eighth tooth position.

Teeth, as exemplified by MAL-176 (height = 27 mm, length = 8 mm, width = 5 mm; Text-figs 1D, 2A) are not broadly spatulate as in *Brachiosaurus* or *Camarasaurus*. The surface of the teeth is rugose and the lingual side is less convex than the buccal side. The distal and medial edges are well defined and sharp, extending from the apex of the tooth. A faint furrow on the buccal surface parallels the medial and distal edges as in *Camarasaurus* and *Brachiosaurus*. The enamel is thin at the base of the crown. The maximum width of the crown is closer to the tip than the base. The crown is straight. While these teeth are not spoon-shaped, neither can they appropriately be termed pencil-like.

One cervical vertebra (No. 89–78; centrum length = 386 mm, centrum height = 110 mm, maximum preserved height of centrum and spine = 410 mm; Text-fig. 1E) has been prepared sufficiently for description. The centrum is opisthocoelous. Anterior and posterior zygapophyses do not extend much beyond the level of the end of the centrum. The neural spine is low and not bifurcated. There are no pleurocoels. The lamina supporting the diapophysis is oriented parallel to the long axis of the centrum. The cervical ribs are long and extend posteriorly well behind their associated centrum as thin rods. Isolated fragments of cervical ribs were previously identified erroneously as ornithischian ossified tendons (Jacobs *et al.* 1990).

The most complete and best preserved of the dorsal vertebrae (No. 89–137) is distinctly opisthocoelous



TEXT-FIG. 1. *Malawisaurus dixeyi*; Malawi; Lupata Group, Early Cretaceous; referred material. A, MAL-6; right premaxilla, lateral view. B-C, MAL-174; right dentary, lingual and lateral views. D, No. 90-69; isolated tooth, posterior view. E, No. 89-78; cervical vertebra, right lateral view. F, Nos. 89-123, 89-124; articulated sternal plates, ventral view. G, MAL-142; left ischium, lateral view. Scale bars, for D = 5 mm, for all others = 50 mm.

(centrum length = 200 mm, posterior centrum width = 170 mm, centrum height = 135 mm, height of centrum and spine = 370, width at diapophyses = 530 mm). Wide transverse processes originate fairly low on the centrum and project horizontally. The neural spine is short, simple, transversely broad, and not bifurcated. It has a small central posterior lamina with larger, dorsally flaring lateral laminae. Its position in the dorsal series is unclear.

Anterior caudal vertebrae are distinctly procoelous, thus conforming to the titanosaurid diagnosis. Based on comparisons with *Alamosaurus* (Gilmore 1946, pls 5–8), of the two anterior caudals from Malawi, the more anterior (No. 90–128; centrum length = 128 mm, posterior centrum width = 129 mm, centrum height = 119 mm, height of centrum and spine = 270 mm, width across transverse processes = 190 mm; Text-fig. 2B) is probably from the second or third position. The other anterior caudal (No. 89–79; centrum length = 131 mm, anterior centrum width = 122 mm, centrum height = 106 mm, height centrum and spine = 215 mm, width at transverse processes = 210 mm; Text-fig. 2C) follows closely in the series. It is likely to derive from a position anterior to the seventh caudal. The posterior ball of the centrum is well developed in both, with the greatest bulge in the dorsal half. The more anterior of the two anterior caudal vertebrae has the transverse processes joined to the neural spine by laminae of bone, producing triangular wing-like projections in anterior view. In both anterior caudals, the neural arch is positioned anteriorly on the centrum and the neural spine is low and vertically oriented. The centrum appears asymmetrical in lateral view with the posterior margin deeper than the anterior. In the more posterior of the two vertebrae (No. 89–79), the prezygapophyses extend beyond the cranial limit of the centrum and facets for articulation with the haemal arch at the posterior margin of the centrum are large. The transverse processes, while distinct and well developed, are isolated rods not connected by winglike laminae to the neural spine. Some diplodocids possess mildly procoelous anterior caudals with well-developed wings, but the anterior caudals from Malawi are clearly titanosaurid based on the extreme procoelous and the substantial length of the centra. None of the caudals from Malawi possesses pleurocoels.

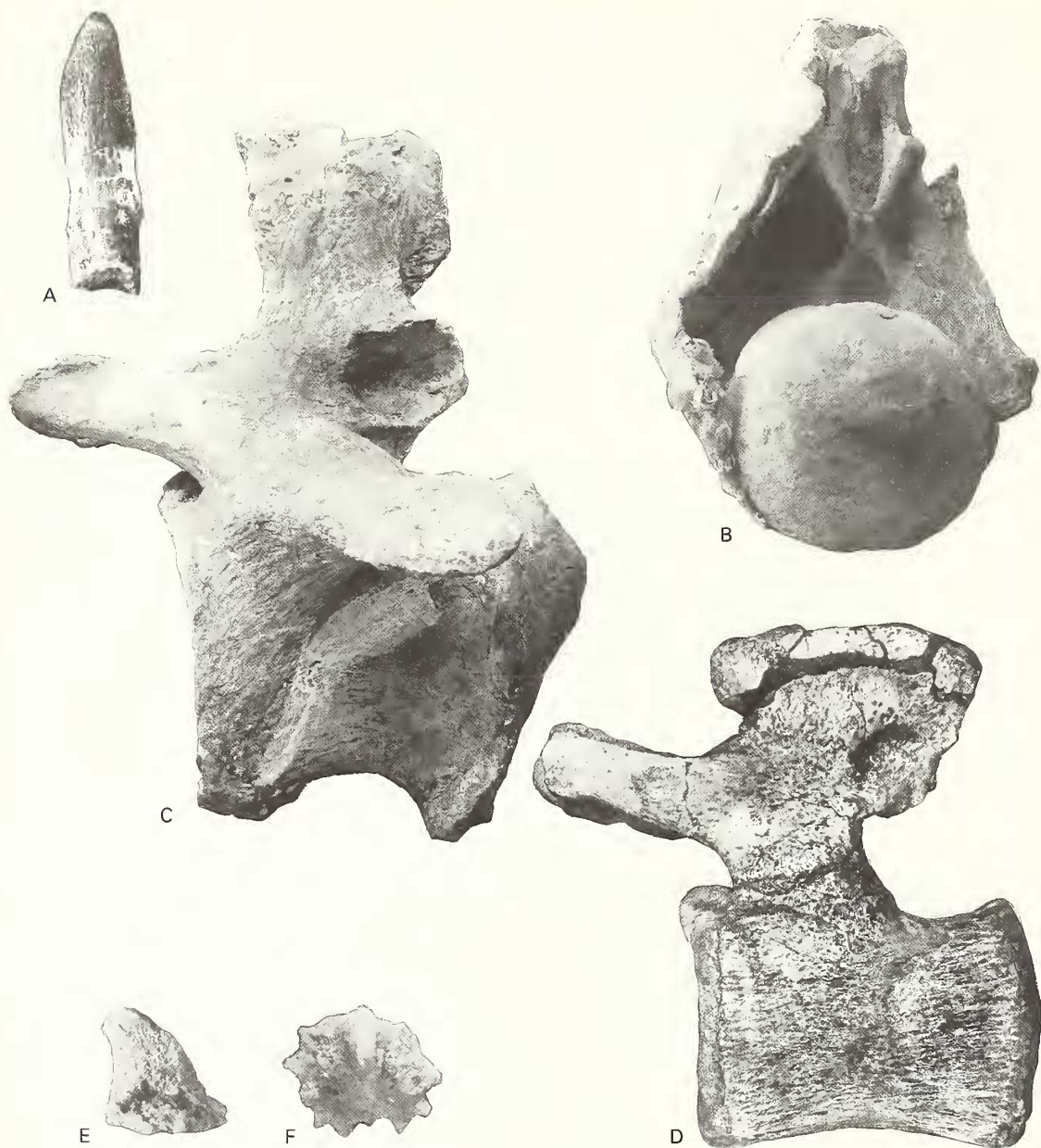
An articulated tail section comprises 22 middle and posterior caudal vertebrae. It shows features consistent with the procoelous anterior caudals, most notably, the neural arches are attached toward the cranial half of the centra, neural spines are low, vertical, and do not extend beyond the posterior margin of the centrum, haemal facets are large, and the prezygapophyses extend well beyond the anterior border of the centrum. Haemal arches are articulated with the centra. They are simple, not bifurcated, and they are longer than the neural spines.

An isolated caudal vertebra (MAL-1; centrum length = 86 mm, posterior centrum width = 57 mm, centrum height = 64 mm, height centrum and spine = 138 mm; Text-fig. 2D) is indistinguishable from that in the 7th position (from the anterior) of the articulated tail section in all essential observable features. Moreover, the centrum of MAL-1 is gently amphicoelous. We consider that MAL-1 represents the same taxon as the articulated tail section. Based on the possession of low vertical spines, strong haemal facets, anteriorly positioned neural arches, and long, anteriorly projecting prezygapophyses, we suggest that the middle and posterior caudal vertebrae belong to the same taxon as the procoelous anterior caudals. This leads to the conclusion that there is a transition from strongly procoelous to gently amphicoelous centra progressing posteriorly along the tail, as will be discussed in more detail below. The short and low neural spines, long prezygapophyses, and long haemal arches that do not bifurcate preclude referral of the articulated tail section to the Diplodocidae.

Sternal plates were found with their anteromedial margins articulated as in life. Each sternal plate flares posterolaterally (Nos 89–123 and 89–124; combined distance across both = 770 mm; Text-fig. 1F). They appear identical in all essential respects to the articulated sternal plates of *Alamosaurus* illustrated by Gilmore (1946, pl. 4b). Haughton (1928, pl. 4 fig. 1) illustrated a sternal plate from Malawi that he assigned to *Gigantosaurus dixeyi*. It is difficult to interpret his illustration or to evaluate the reconstructive preparation, but it appears that if the specimen were rotated clockwise such that the top edge became the medial articulation, it would resemble closely the sternal plates reported here.

A left ischium (MAL-42) has a robust peduncle for articulation with the ilium (Text-fig. 1G). The medial flange for articulation with the pubis is long (157 mm). The ischium distal to the flange is transversely broad (132 mm) relative to total length (390 mm).

Comparisons. Based on the possession of strongly procoelous anterior caudal vertebrae, *M. dixeyi* is clearly a titanosaurid. Some other sauropods (notably *Diplodocus* and to a lesser extent *Apatosaurus*) have anterior caudals that are weakly procoelous (Osborn 1899; Gilmore 1936); but the centra are short relative to those in *Malawisaurus* and other titanosaurids, and the posterior ball is not nearly so well developed. Moreover, the chevrons of diplodocids are sledge-shaped.



TEXT-FIG. 2. *Malawisaurus dixeyi*; Malawi; Lupata Group, Early Cretaceous; referred material. A, MAL-176, isolated tooth, lingual view, $\times 1.28$. B, No. 90-128; anterior caudal vertebra, posterior view, $\times 0.28$. C, No. 89-79; anterior caudal vertebra, left lateral view, $\times 0.46$. D, MAL-1; middle caudal vertebra, left lateral view, $\times 0.56$. E-F, calcite pseudomorphs presumed to represent dermal ossicles, lateral and dorsal views, $\times 1.3$.

Bellusaurus sui from the Middle Jurassic of China is reported to have procoelous anterior caudals and amphicoelous middle caudals (Dong 1990). We have not examined the material so comments must be based on the published English summary and illustrations. *Bellusaurus* appears to be primitive in having undivided neural spines on anterior dorsal and cervical vertebrae, in the narrow

outline of the ischium, and perhaps in the width of the teeth. While it was assigned to the Brachiosauridae, the possibility that *Bellusaurus* may be the oldest known titanosaurid cannot be ruled out.

M. dixeyi is similar to *Janenschia robusta* from the Late Jurassic of Tendaguru, Tanzania. McIntosh (1990a, 1990b) considered it to be unsettled whether *Janenschia* is a titanosaurid. The problem stems from the lumping of a series of caudal vertebrae, which are strongly procoelous in the anterior portion of the tail, with type material from another locality that includes no caudal vertebrae (Janensch 1922, 1961). We assume the association of the Tendaguru caudal series having procoelous anterior centra with the name *Janenschia robusta* to be valid. In any event, meaningful comparisons with the caudal series from Tendaguru can be made, regardless of its binomial, and that tail specimen, at least, in our opinion pertains to the Titanosauridae.

While the caudal series assigned to *Janenschia* is strongly procoelous anteriorly (Janensch 1929, fig. 16), by approximately the 12th to 15th caudal position the posterior ball of the centrum is much less pronounced than in the vertebrae nearer the cranial end, and the ball is lost completely towards the end of the tail. The posterior caudal vertebra illustrated by Janensch (1929, fig. 19a) is not procoelous. These vertebrae, if correctly identified, demonstrate the transition from strong procoely to gentle amphicoely in the tail of *Janenschia*. *Malawisaurus* is similar to *Janenschia* in this feature. The transition from procoely also appears in *Bellusaurus* and in some diplodocids as mentioned above, although diplodocid anterior caudals are not strongly procoelous.

Malawisaurus is distinct from *Janenschia* in having lower erect caudal neural spines that do not project beyond the posterior margin of the centrum and elongate prezygapophyses that extend well beyond the anterior margin. The cervical vertebra referred to *Janenschia* by Janensch (1929, fig. 9) differs from *Malawisaurus* in having irregular pleurocoels. The ischium of *Janenschia* (Janensch 1961, pl. 19, fig. 7) is less transversely expanded than that of *Malawisaurus*. In the transition from procoely to amphicoely along the tail, the two genera are primitive among titanosaurids. In the features in which the two differ, *Malawisaurus* appears derived.

Raath and McIntosh (1987) assigned a series of caudal vertebrae, a humerus, and an incomplete femur from the Kadzi Formation, Zimbabwe, to *Tornieria* (now *Janenschia*). The caudal vertebra that they illustrated [figs 5a(ii), 5a(iii)] is definitely titanosaurid based on its procoely. The humerus is more robust than undescribed specimens from Malawi and more like some of those from Tendaguru. If the associations at Kadzi, Tendaguru, and northern Malawi are correct, the Kadzi titanosaurid is more like *Janenschia* than *Malawisaurus*.

The age of *M. dixeyi* makes it the only known African Early Cretaceous titanosaurid, and it is among the most completely known titanosaurids of that age. The report of titanosaurids from the Early Cretaceous of Gadoufaoua, Niger, while based on apparently excellent material, utilizes a two-fold familial division of the sauropods, which includes diplodocids (*sensu* McIntosh 1990a) in the Titanosauridae. The description of the Gadoufaoua material (Taquet 1976) clearly indicates diplodocid, rather than titanosaurid, affinities in the sense that these terms are used here.

Titanosaurid fossils are known from the Late Cretaceous of Africa. *Aegyptosaurus bahariensis* was described by Stromer (1932). Stromer's illustrations (figs 4a–c) indicate that the caudal vertebrae were procoelous at least through the middle portion of the tail. Other specimens from North Africa referred to *Aegyptosaurus* (Lapparent 1960, pl. 6, fig. 8) are fragmentary but also show that procoely extend at least to the middle caudal vertebrae. Two titanosaurid vertebrae were reported from the Late Cretaceous of False Bay, South Africa (Kennedy *et al.* 1987).

Malawisaurus is distinct from all other Cretaceous dinosaurs of Africa, so far as can be determined. The Late Cretaceous *Rebbachisaurus* comprises two species. The type, *R. garasbae* from Morocco, includes a dorsal vertebra with large pleurocoels and a long neural spine. The second species, *R. tamesnensis* from Niger, has broad *Camarasaurus*-like teeth anterior dorsal vertebrae with a bifurcated neural spine, and an ischium without transverse expansion, if all the specimens are correctly allocated (Lapparent 1960, pl. 10, fig. 2, pl. 11, fig. 3). These species are not titanosaurid. McIntosh (1990a) considered it plausible that *Rebbachisaurus garasbae* is a diplodocid.

Algoasaurus bauri from South America is a *nomen dubium* (McIntosh 1990a). Its age is uncertain,

but is either Late Jurassic or Early Cretaceous (Mateer *et al.* 1992). The type material is fragmentary. The original description (Broom 1904, p. 447) mentions that it has the 'peculiar excavations seen in the centra of the American types' (presumably = pleurocoels). Broom's line drawing (fig. 2) shows a fragmentary vertebra, identified as a posterior dorsal, with an undivided neural spine. The teeth of three sauropod taxa were identified from the same formation that yielded *Algoasaurus* (Rich *et al.* 1983): aff. *Astrodon* sp., aff. *Pleurocoelus* sp., and aff. Camarasauridae. Judging from the variation that has been documented in the teeth of *Brachiosaurus* (Janensch 1935), for the sake of heuristic argument, we suggest that these teeth exhibit no more variation than might reasonably be expected in a single sauropod taxon. Further, affinities of *Algoasaurus*, and the South African teeth might lie with *Rebbachisaurus*.

Titanosaurid material from the Late Cretaceous of Europe (*Magyarosaurus*, *Hypselosaurus*), India (*Titanosaurus*), and Madagascar (*Titanosaurus* or *Laplatasaurus*) is incomplete. Middle and distal caudals are procoelous where representative bones are known, thus distinguishing the Late Cretaceous forms from *Malawisaurus*. *Macrurosaurus* from the Early Cretaceous of Europe is poorly known, but the caudal centra show a transition from strongly procoelous to gently amphicoelous or flattened (Seeley 1876).

The oldest known and most primitive New World titanosaurid is *Andesaurus* from the Albian or Cenomanian of Argentina. Based on the pelvis, it is a titanosaurid, but no anterior caudal centra are known. The more posterior caudals are amphiplatyan (Calvo and Bonaparte 1991, fig. 4A–C). It is similar to *Malawisaurus* in this feature, but the ischium (Calvo and Bonaparte 1991, fig. 5A) is not so transversely expanded as in the African form. If *Andesaurus* is truly a titanosaurid, it is significant in that it is the only known South American genus lacking procoelous posterior caudal centra, and it is as primitive as African *Janenschia* and *Malawisaurus* in that character.

Comparisons with Late Cretaceous titanosaurids from the Americas are facilitated by higher quality samples, especially of *Saltasaurus* in South America (Bonaparte and Powell 1980) and *Alamosaurus* in North America (Gilmore 1922, 1946). *Malawisaurus* is distinct from, and primitive relative to *Saltasaurus*, *Laplatasaurus*, *Argyrosaurus* and *Alamosaurus* in having gently amphicoelous, rather than procoelous, middle caudal centra. It is similar in having low caudal neural spines, transversely expanded ischia, and large sternal plates. One character that may eventually prove to be a synapomorphy among American titanosaurids is the possession of a biconvex centrum in the first caudal vertebra, a character known only in *Alamosaurus* and at least some South American titanosaurids so far as it can be evaluated.

Special mention must be made of the South American genus *Antarctosaurus*, which has been considered a titanosaurid, because Huene (1929) assigned a lower jaw fragment (pl. 29, figs 4–5) and some teeth (pl. 29, fig. 3) to this taxon. The teeth are pencil-like, although they are slightly flattened, and the jaw fragment has an anteriorly restricted tooth row with an abrupt angle towards the symphysis. These characters are certainly similar to *Diplodocus*, thus influencing reconstructions of titanosaurids and resulting in the lumping of titanosaurids with diplodocids, even to the extent that in Romer's (1956) classification, the sauropods comprises only two families, the Brachiosauridae and the Titanosauridae.

The features of *Malawisaurus* contradict an especially close relationship of titanosaurids with diplodocids. The teeth of *Malawisaurus* are more narrow than in *Brachiosaurus*, but they are not pencil-like. Broad, leaf-shaped teeth are primitive for sauropods. Teeth referred to *Alamosaurus* are transversely rounded and elongate (Kues *et al.* 1980, fig. 2), the morphology referred to as pencil-like in sauropods, as are others illustrated by Huene (1929, pl. 1, figs 12–13), which possibly pertain to *Saltasaurus* or *Laplatasaurus*. On the other hand, the teeth of *Camplodoniscus* (= *Campylodon*) illustrated by Huene (1929, pl. 40, figs 1–2) are Late Cretaceous South American sauropod teeth that are clearly not pencil-like. McIntosh (1990a) considered *Camplodoniscus* to be *incertae sedis*.

Pencil-shaped teeth are derived, but the morphological change from broad to narrow teeth is so simple that convergence would be hard to document based on a comparison of end members. Considering the morphology of *Malawisaurus* teeth, we conclude that 'pencil-like' teeth evolved at least once in the Titanosauridae and in parallel at least once in the Diplodocidae.

The jaw fragment assigned to *Antarctosaurus*, with its pencil-like teeth, resembles diplodocids because of its angulation toward the symphysis and its restricted tooth row. We consider it less likely that titanosaurids and diplodocids would evolve those characters in parallel. Caudal vertebrae of *Antarctosaurus* are unknown. There are no features on any of the bones illustrated by Huene that exhibit any derived characters of titanosaurids, including the distal ischium (Huene 1929, pl. 32, fig. 3), which would be expected to be more expanded. Therefore, based on the morphology of the *Malawisaurus* jaw, which is dissimilar albeit primitive relative to diplodocids, and the lack of derived titanosaurid features on other known parts of *Antarctosaurus*, the referral of *Antarctosaurus* to the Titanosauridae can be questioned, even if not fully refuted.

Antarctosaurus is possibly a diplodocid, a family which is not otherwise known from the Late Cretaceous of South America. A derived diplodocid, *Amargasaurus*, is known from the Early Cretaceous of Argentina (Salgado and Bonaparte 1991). No bones in South America from the Late Cretaceous other than the lower jaw of *Antarctosaurus* exhibit definite diplodocid synapomorphies (e.g. sledge-shaped chevrons, bifurcated cervical neural spines). In fact, their only other Late Cretaceous records are in Asia (McIntosh 1990a), those being the highly derived genera *Nemegtosaurus* and *Quaesitosaurus*.

The referral of *Antarctosaurus*, with its diplodocid jaw structure, to the Titanosauridae led to the persistent misconception that titanosaurid skulls should be similar in structure to diplodocid skulls. This caused further confusion when *Antarctosaurus* was identified in India by Huene and Matley (1933). In that same paper a sauropod maxilla was described, but it was considered of uncertain genus and not identified to any lower level. The salient features of the Indian maxilla, as shown by the figure and description in Huene and Matley (1933, p. 23, fig. 19), are the vertical orientation of the ascending process separating the external naris from the antorbital fossa, and the position of the maxillary-premaxillary suture. They clearly stated (p. 24) 'very little of the anterior margin is missing'. The entire length of the suture appears to lie beneath the external naris, not anterior to it.

We agree with Huene and Matley (1933, p.24), based on their figure and description, that the Indian maxilla represents a sauropod in which 'the snout was short and very high', and we further suggest that it is the maxilla of a titanosaurid. The suggestion is made because the only other sauropod specimen known that exhibits a maxillary-premaxillary suture entirely beneath the external naris is the premaxilla of *Malawisaurus* from Africa.

Dermal armour

One of the most intriguing features of titanosaurids is the presence of dermal ossicles, known from Madagascar (Depéret 1896) and South America (Bonaparte and Powell 1980). No bones have been found in Malawi that can be said with certainty to be dermal ossicles. However, in the same quarry with titanosaurid bones are calcite pseudomorphs with a shape remarkably like dermal armour (Text-fig. 2E-F). In addition, calcite fills the marrow cavities of some of the long bones. The pseudomorphs have a subcircular base, concave on one side, but with a tall keel on the other. The base is flattened on one edge and the perimeter is ornamented with 12 to 13 small projections. The pseudomorphs are bilaterally symmetrical with the spine being compressed and inclined towards the flattened edge of the base, which is taken to be posterior. These pseudomorphs appear to be biological in origin, and it is worth speculating that they may represent titanosaurid dermal ossicles. The description and illustrations of the osteoderms of *Saltasaurus* (Bonaparte and Powell 1980, fig. 6) indicate a ventrally cupped base with a keeled upper surface in some specimens.

DISCUSSION

Janenschia robusta from the Late Jurassic of Tendaguru, Tanzania, has traditionally been recognized as the oldest titanosaurid, and therefore, the family has been considered to be of African origin. It may have had such an origin, but the description of *Bellusaurus* from the Middle Jurassic

of China, at a minimum, suggests alternatives. Until the Jurassic record is more fully known, the question of where titanosaurids originated remains open.

By the Early Cretaceous, titanosaurids had spread to Europe. The terrestrial record for the Early Cretaceous is poor in South America, but *Andesaurus* is possibly of that age and it lacks procoelous posterior caudal centra, as does *Malawisaurus*. After South America and Africa split apart, South America's titanosaurid fauna entered a period of approximately 30 million years of evolution in isolation from the influence of other continents.

Late Cretaceous titanosaurids from Madagascar and India may represent remnants from before the separation of these land masses from Gondwana, or they may indicate a more complicated geographical pattern. Currently, titanosaurids from those places are not sufficiently well known for their geographical history to be understood. The geographical origin of *Alamosaurus*, the only known North American titanosaurid, is clearer. Titanosaurids, in all probability, migrated up from South America near the end of the Cretaceous at the same time ceratopsians, hadrosaurs, and marsupials were invading South America from the north (Bonaparte 1984, Rage 1986). Then, at the end of the Cretaceous, just a few million years after it reached North America, *Alamosaurus*, possibly the last of the titanosaurids (and if so, the last of the sauropods) became extinct.

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